

Due to the lack of data on *Hapalopsittica* species our data can only be compared to other similar sized parrots such as *Pionopsitta* species (Forshaw 1989). The Pileated Parrot *Pionopsitta pileata* has an incubation period of 24 days (*cf.* Red-faced Parrot: 26–29 days), fledging between 52–54 days of age (*cf.* Red-faced Parrot: 49–52 days) and self-feeding when 57–59 days old (Forshaw 1989). These data suggest that the Red-faced Parrot's incubation and fledging periods are similar to those of other parrots of similar size.

The fact that Red-faced Parrots feed on common Andean plant genera such as *Miconia*, *Myrcianthes*, *Weinmannia* and *Clethra* suggests that their restricted range and their rarity are not due to a dependence on certain foods. However, they may require special plants at certain times such as their breeding season. For example in October, the pre-laying period of most birds in the yungas of Cochabamba, Bolivia, Black-winged Parrots *Hapalopsittica melanotis* were found to specialise on the fruits of cloud-forest mistletoes of the genus *Gaiadendron*, which may represent a high-nutrition food source (J. Fjelds  in litt. 1993).

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# The history and taxonomic status of the Hispaniolan Crossbill *Loxia megaplaga*

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In October 1916, W. L. Abbott collected a pair of hitherto unknown and unexpected crossbills near El Rio, in the Cordillera Central of the Dominican Republic, on the West Indian island of Hispaniola. These were described by Riley (1916) as *Loxia megaplaga* (holotype USNM 249515), and were compared in plumage and morphology primarily with the palearctic *L. bifasciata*, then generally considered a species distinct from the nearctic *L. leucoptera*, the White-winged Crossbill (but see Hartert 1910). In his comments, Riley asserted that *megaplaga* "can be told at a glance" from *leucoptera* by its heavier, less attenuated bill, a difference further discussed and illustrated by Richmond (1916). As he was leaving Hispaniola, Abbott encountered Rollo Beck, then collecting for the Brewster-Sanford Collection. Told by Abbott of this and other interesting discoveries, Beck spent much of late February and March 1917 in the Cordillera Central (Beck 1921), eventually securing a series of thirty-one specimens of *megaplaga*, including several recent fledglings. Twenty-three of these are now at the American Museum of Natural History and four are at the British Museum (Natural History). In a search of likely museums I was able to learn of less than ten specimens taken subsequently, suggesting that fewer than fifty exist.

When Beck's series came to the attention of Frank Chapman at the American Museum of Natural History, Chapman described the discovery as "one of the ornithological sensations of recent years" (Chapman 1917). After saying that he had no specimens of *bifasciata* for comparison, he speculated how a "race" (Chapman's word, although he maintained binomial nomenclature and referred to it as a "species" elsewhere in his note) of the North American White-winged Crossbill *leucoptera* (*s.s.*) could occur in such a remote, tropical environment. He suggested that White-winged Crossbills, as well as the pines to which they were adapted (*sic, infra*), may have been more widespread during the previous ice age. Neither Bond (1928), Wetmore & Swales (1931), nor the A.O.U. (1931) considered *megaplaga* (or *bifasciata*) to be a subspecies of *leucoptera*, although Wetmore & Swales (1931) stated that "Obviously the three are from common stock".

The first explicit treatment of *megaplaga* as a subspecies of *leucoptera* (*s.l.*) seems to have been by Hartert & Steinbacher (1932). Bond (1936) also used trinomial treatment, as did Hellmayr (1938), although neither cited Hartert & Steinbacher (1932); Griscom (1937), on the other hand, did so. The A.O.U. formally adopted subspecific treatment for *megaplaga* several years later (A.O.U. 1944), citing Hellmayr (1938). It is not evident that any of those authors were expressing other than the emergent taxonomic philosophy of the era, which focused more on apparent similarities between taxa than differences. Bond (1945) wrote,

“The presence of a White-winged Crossbill in Hispaniola is probably the result of an invasion of the species during the Pleistocene”, a notion for which Chapman (1917) apparently laid ground and which Wetmore & Swales (1931) had developed further.

Griscom (1937) is the principal author to have analysed the alignment of *megaplaga* with *leucoptera*, his discussion also including *bifasciata*. He rejected six of nine possible criteria proposed by other authors to diagnose *L. leucoptera* (*s.l.*) from *L. curvirostra* (*s.l.*) as overlapping: smaller size and bill; proportionately more slender bill; pinker or paler shades of red in adult males; yellower olive tones in adult females; two well-developed white wing-bands (!); and different breeding and winter plumage of adult males. He accepted only broad white tips to the tertials, blackish remiges and rectrices, and black upper tail coverts as characters shared by all forms of *leucoptera* and no forms of *curvirostra*.

Meanwhile, *megaplaga* largely slipped from ornithological consciousness. It apparently went unreported in field literature for the forty years following Bond's collecting five in Haiti in 1930 (unpublished, M. Robbins *in litt.*). Annabelle Stockton Dod then claimed to “rediscover” crossbills on Hispaniola in 1971 in the Sierra de Baoruco, an extension of the Haitian Massif de la Selle into the southwestern Dominican Republic (Dod 1978). In fact, J. W. Terborgh had reported them both there and in the Cordillera Central a year earlier (Bond 1971). In April 1971, Dod and the Keplers found the first nest of *megaplaga* recorded, near the Dominican-Haitian border in those same mountains (Kepler *et al.* 1975). At least three crossbills identified carefully and credibly as *megaplaga* were observed in introduced pines in the Blue Mountains of Jamaica for several months beginning in December 1970 (Lack *et al.* 1972, notwithstanding Bond's 1972 disbelief), where no species of pine is native. There apparently are no other known reports of crossbills in Jamaica (R. Sutton) or elsewhere in the West Indies.

Since its “rediscovery”, *megaplaga* has been reported occasionally in the Dominican Republic by resident and visiting birdwatchers and scientists, both in the Cordillera Central and the Sierra de Baoruco. Because of near total deforestation, its current status in Haiti is uncertain, although apparently it is not completely extirpated there (Benkman 1994). Benkman (1994) observed and studied its morphology and ecology in the Dominican Republic and concluded that it was a specialist adapted to forage solely on *Pinus occidentalis*, Hispaniola's sole native conifer, found only there and in the Sierra Maestra of Cuba (Sauget & Liogier 1946, Mirov 1967). He suggested that its bill structure was so different from *leucoptera* (*s.s.*), primarily a spruce-feeding specialist (Benkman 1992), that hybrids would be selectively disadvantaged (Benkman 1994). Benkman (1994) computed a likely population size for *megaplaga* of less than 1000 remaining individuals.

In March, 1996, assisted by tape playback of vocalizations which Reynard (1981) secured both in Haiti and near El Aguacate, Dominican Republic (G. Reynard *in litt.*), L. Manfredi and I searched unsuccessfully for crossbills for five days between *c.* 700 and 1200 m in

the Cordillera Central within *c.* 50 km of Jarabacoa, including the area of El Rio where most of Beck's specimens had been taken. Although there still are many patches of pines in that region, few remaining trees appear to consist of old growth. An intensive two-year study in a portion of the area we surveyed failed to encounter the species (Latta & Wunderle 1996), although ornithologists working in the area's pines occasionally do encounter crossbills (Benkman 1994, J. Wunderle). Then moving to the Sierra de Baoruco on 26 March to the vicinity of the abandoned Zapotén logging camp, 5 km south of El Aguacate on the Haitian border at *c.* 1500 m, we attracted a family group of crossbills (male, female, and three juveniles) to our location within a few minutes of our arrival in an area of old growth by playing the Reynard (1981) recording.

We made leisurely telescopic studies for about an hour between 8–9 a.m. Our most unexpected observation in light of Griscom's (1937) diagnosis of *leucoptera* (*s.l.*) including *megaplaga*, was that the remiges, rectrices, and upper tail coverts did not appear "blackish" but instead appeared brown, and the tertials of the adults did not seem at all white-tipped (those on the juveniles were narrowly edged with white). Other characters noted included the massive beaks and the fact that the greater covert tips seemed only narrowly white, narrower than the median covert tips. The birds seemed remarkably silent for crossbills, although the male did warble faintly for lengthy periods as we watched. Their principal vocalizations, made occasionally during their slow approach to our vicinity as we played the recording, were aurally indistinguishable to us from those published by Reynard (1981).

I examined the series of twenty-three specimens of *megaplaga*, all secured by Beck, at the American Museum of Natural History. Susan A. Smith and I took measurements of most adults (Table 1), and to the extent specimens were available, we also took equivalent measurements of a comparable number of adult *leucoptera* (*s.s.*), *bifasciata*, and *Loxia curvirostra mesamericana*, the geographically nearest member of *Loxia*, which is found primarily in pine forest from Guatemala to Nicaragua (Howell *in* Paynter 1968). Additionally, through the courtesy of Brian Nelson, I obtained sonagrams of *megaplaga*'s basic vocalizations from Reynard (1981) (Fig. 1).

In comparing the series of *megaplaga* with those of other crossbill taxa, I failed to discern that *megaplaga* (or *bifasciata*) had blackish remiges, rectrices, or upper tail coverts, *contra* Griscom (1937). My judgement was that all *Loxia* have those feathers concolorous. *Leucoptera*'s (*s.s.*) indeed are black, but all other taxa are shades of brown, those of *bifasciata* appearing hardly darker than most *curvirostra*'s and lighter than some. *Megaplaga*'s feathers are a darker shade of brown than *bifasciata*'s. Adult *megaplaga* in series also lack prominent white tertial tips as shown by many *leucoptera* (*s.s.*) and *bifasciata*. I thus concluded that the specimens of *megaplaga* generally agreed with my field observations, but not with Griscom's (1937) museum basis for including *megaplaga* within *leucoptera* (*s.l.*), a discrepancy I cannot explain inasmuch as the same material was largely used.

TABLE 1  
Measurements of adult Hispaniolan Crossbills

| Catalog no. | Date      | Sex | Bill   |       |       | Volume index | Wing | Tail | Wing:tail | Width gr. cov. tips |
|-------------|-----------|-----|--------|-------|-------|--------------|------|------|-----------|---------------------|
|             |           |     | Length | Width | Depth |              |      |      |           |                     |
| AMNH 164844 | 19/3/1917 | M   | 17.05  | 6.34  | 10.93 | 11.82        | 88   | 57   | 1.54      | 4.14                |
| AMNH 164845 | 2/3/1917  | M   | 16.93  | 6.66  | 11.69 | 13.18        | 89   | 58   | 1.53      | 3.61                |
| AMNH 164847 | 5/3/1917  | M   | 16.97  | 7.28  | 11.25 | 13.90        | 88   | 56   | 1.57      | 4.34                |
| AMNH 164848 | 23/2/1917 | M   | 17.16  | 6.10  | 11.30 | 11.83        | 87   | 58   | 1.50      | 3.62                |
| AMNH 164849 | 23/2/1917 | M   | 17.05  | 7.08  | 11.02 | 13.30        | 90   | 59   | 1.53      | 4.01                |
| AMNH 164851 | 2/3/1917  | F   | 16.38  | 7.28  | 10.66 | 12.71        | 88   | 55   | 1.60      | 2.86                |
| AMNH 164855 | 10/3/1917 | F   | 16.75  | 7.32  | 10.58 | 12.97        | 84   | 56   | 1.50      | 3.40                |
| AMNH 164857 | 16/3/1917 | F   | 16.26  | 6.93  | 11.01 | 12.41        | 83   | 53   | 1.57      | 3.58                |
| AMNH 164858 | 10/3/1917 | F   | 16.54  | 6.60  | 10.65 | 11.63        | 86   | 56   | 1.54      | 3.54                |
| AMNH 164859 | 5/3/1917  | F   | 15.49  | 7.08  | 10.55 | 11.57        | 82   | 53   | 1.55      | 0.88                |

TABLE 2  
Summary (mean, s.d.) measurements of adult crossbills

| Taxon                | n  | Bill volume index | Greater covert tips | Wing       | Tail       | Wing:Tail   |
|----------------------|----|-------------------|---------------------|------------|------------|-------------|
| <i>megaplaga</i>     | 10 | 12.53, 0.767      | 3.40, 0.927         | 86.5, 2.54 | 56.1, 1.92 | 1.54, 0.030 |
| <i>bifasciata</i>    | 9  | 9.64, 2.456       | 8.18, 2.198         | 90.8, 2.48 | 60.2, 1.47 | 1.51, 0.040 |
| <i>leucoptera</i>    | 9  | 5.93, 0.711       | 9.75, 1.977         | 86.0, 3.37 | 59.6, 2.01 | 1.44, 0.044 |
| <i>mesamerticana</i> | 6  | 12.50, 1.148      | N/A                 | 93.8, 3.29 | 52.8, 0.90 | 1.78, 0.060 |

Note. Measurements in mm. Bill volume index =  $L \times W \times D/100$ .

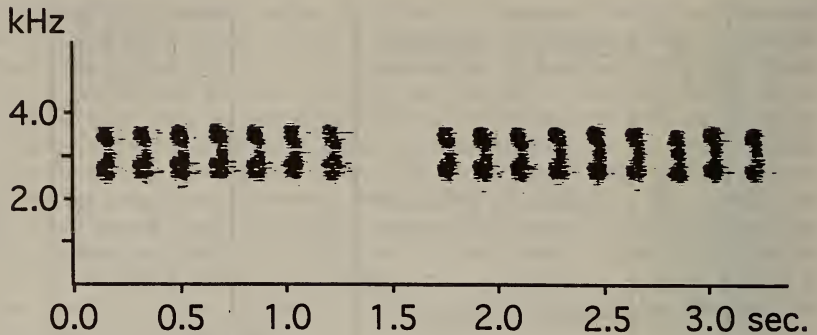


Figure 1. Hispaniolan Crossbill vocalizations (from Reynard 1981).

Unlike either *leucoptera* (*s.s.*) or *bifasciata*, *megaplaga* has relatively narrow white tips to the greater coverts (Table 2), with most such feathers being medially dark almost to the edge. This character agrees more with the rare, so-called '*rubrifasciata*' morph of *curvirostra* (Eck 1981, Cramp & Perrins 1994). But for the presence of wingbars, the only morphological character of *megaplaga* that suggests commonality with *leucoptera* (*s.l.*) is the wing:tail ratio (Table 2, Eck 1981). Even that feature is somewhat ambiguous, however, for *megaplaga*'s ratio is larger than either *leucoptera*'s (*s.s.*) or *bifasciata*'s (nearer the latter than the former) and begins to approach the various forms of *curvirostra* (*s.l.*) (Table 2, Eck 1981, Cramp & Perrins 1994).

The vocalizations of *megaplaga* (Fig. 1) consist mainly of a series of somewhat harmonic 100 ms notes *c.* 1.2 kHz in range, centred at *c.* 3.1 kHz and uttered at a rate of *c.* 5.5/sec. Among the several calls of *leucoptera* (*s.s.*) documented by Munding (1979), the "chutter" consists of notes structurally similar to those of *megaplaga* but of about one-fourth the duration delivered about four times as fast. All other calls recorded by Munding (1979) are more different structurally. The song of *leucoptera* (*s.s.*) shown in Cramp & Perrins (1994) consists mainly of similar-structured notes of slightly higher frequency than those of *megaplaga*, delivered about twice as fast. I am uncertain whether the vocalizations of *megaplaga* on Reynard (1981) or heard by us should be characterized as "song" or "calls". The calls of *bifasciata* documented in Cramp & Perrins (1994) have more harmonic qualities, are longer and are given more slowly than vocalizations of *megaplaga*, but span roughly the same frequency. Munding (1979) argues that vocalizations of carduelines are learned in a social context, thus one would expect those of modern isolated *megaplaga* to have drifted from their progenitor. Although Groth (1993) did not study vocalizations of *mesamericana*, none of the calls of North American *curvirostra* (*s.l.*) that he did document seem as similar structurally to those of *megaplaga* as were those of either *leucoptera* (*s.s.*) or *bifasciata*.

Bond (1945) and others supposed that *megaplaga* was a relict of a Pleistocene irruption of *leucoptera* (*s.s.*). While one cannot dismiss such

a theory, no particular evidence supports it. Bond's (1940) supposition that *megaplaga's* presence on Hispaniola "... is probably due to some accidental invasion in the past, the birds becoming established on finding conditions suitable" failed to recognize *leucoptera's* (*s.s.*) adaptation to *Picea* (Benkman 1992). *Megaplaga* is the only member of *leucoptera* (*s.l.*) adapted to feed on large cones of *Pinus* (Benkman 1994). Mirov (1967) found chemical similarities between Hispaniolan *P. occidentalis* and various species of pine found in central and western North America which are lacking from all pine species found in eastern North America. Thus, *P. occidentalis* probably evolved from mesamerican pine stock. It seems plausible, therefore, that *megaplaga* either evolved *in situ* or colonized from a Central American ancestor. It is striking that *megaplaga's* bill is rather similar in size to *mesamericana* (Tables 1, 2), which suggests a common ancestor or convergence due to similarity in cone structure of the resident pines. Its ancestor may have been unlike modern *leucoptera* (*s.s.*), which may have evolved its spruce-adapted bill structure *after* that supposed invasion, given that there is no evidence that small-coned conifers ever were present in the West Indies.

In plumage and morphology, *megaplaga* reflects a mosaic of characters found in *Loxia*. As recognized by its describer (Riley 1916), it shows more morphological similarity to the palearctic *bifasciata* than the nearctic *leucoptera* (*s.s.*). The colour of its flight feathers and the width of the white on its greater covert tips are intermediate between *leucoptera* (*s.s.*) and *curvirostra* (*s.l.*). Its wing:tail ratio is closer to *leucoptera* (*s.l.*) than to *curvirostra* (*s.l.*) but is intermediate and more like *bifasciata* than *leucoptera* (*s.s.*). It shows morphological similarity to the Central American Red Crossbill *L. curvirostra mesamericana* but with 'rubrifasciata'-like wingbars and a smaller wing:tail ratio. Its vocalizations are more like *leucoptera* (*s.l.*) than any population of *curvirostra* (*s.l.*) for which recordings are available (Mundinger 1979, Groth 1993, Cramp & Perrins 1994).

The evolutionary history of *megaplaga* can be unravelled with certainty only by use of genetic techniques. Nevertheless, it now is so isolated spatially, morphologically, and ecologically from *leucoptera* (*s.s.*) (Benkman 1994, this study) that nothing seems served by combining it with *bifasciata* and *leucoptera* into a composite species which is questionably diagnosable (Griscom 1937, this study). I therefore agree with Benkman (1994) that *Loxia megaplaga* should be recognized as a full species, the Hispaniolan Crossbill, as it was described originally.

Such recognition might also help bring more attention to this evidently endangered taxon. Nothing in my travels in the Dominican Republic since 1987 has led me to believe that Benkman's (1994) population estimate of under 1000 individuals was unduly pessimistic. Most reports of *megaplaga* since 1970 have been along the Haitian border in the Sierra de Baoruco. Although this region is gazetted as National Park, there seems to be no active protection. I observed widespread poaching of trees by Haitians, who widely lack their own trees, and several active charcoal-making sites along the border in the